Leaf water relations of cotton in a free-air CO_2-enriched environment

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Abstract

As part of an intensive study of crop response to CO_2 enrichment in a free-air CO_2 enrichment (FACE) experiment in the field, we determined aspects of the water relations of a cotton crop on selected dates in 1991. The atmosphere was enriched from 370 μmol CO_2 mol^{-1} (control) to about 550 μmol mol^{-1} in free air during daylight hours. Under full irrigation, CO_2 enrichment decreased stomatal conductance and single-leaf transpiration only toward the end of the season, and these changes led to increased leaf water potentials only at that time of year. Under water-stressed (deficit irrigation) conditions, CO_2 enrichment decreased conductance throughout the season but there was no corresponding consistent effect on leaf water potentials. As with the fully irrigated controls, CO_2 enrichment increased leaf water potentials only at the end of the season. CO_2 enrichment increased season-long biomass accumulation 39% under full irrigation and 34% under deficit irrigation. These results are consistent with previous studies of cotton in open-top chambers that found only small effects of CO_2 enrichment on internal water relations of cotton, and no water stress-induced increase in crop responsiveness to elevated CO_2.

1. Introduction

The CO_2 concentration of the atmosphere has been increasing since the late

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nineteenth century, and is expected to continue increasing for the forseeable future. This change is of interest to agriculture because CO_2 is the raw material for the photosynthetic production of crop biomass, and availability of CO_2 can be an important limitation to productivity. In most crops, atmospheric CO_2 enrichment stimulates photosynthetic rate, growth, and yield, although the degree of stimulation varies depending on such factors as plant type, developmental stage, environment, and nutritional status (Kimball, 1983, 1985; Jones et al., 1984; Strain and Cure, 1986; Hileman et al., 1992; for recent reviews, see Bhattacharya, 1993; Bowes, 1993). In addition, CO_2 enrichment often slows transpiration rate by partially closing stomata, thereby restricting the diffusion of water vapor from the leaf to the atmosphere (Bhattacharya, 1993; Bowes, 1993).

Most studies of CO_2 responses have been carried out in controlled environments (glasshouses or growth chambers). There are several reasons to question whether results from typical controlled environments might be applicable to the field; for example, growing plants in pots causes artificial restriction of rooting (Thomas and Strain, 1991), and the thermal environment is modified compared with that in the field (Radin et al., 1987). To overcome such deficiencies, some investigators have grown crops in CO_2-enriched open-top chambers in the field (Rogers et al., 1984; Kimball et al., 1986; Bhattacharya et al., 1990; Kimball and Mauney, 1993). Results with cotton (*Gossypium hirsutum* L.) differed from those obtained in controlled environments. Over several years, the degree to which CO_2 enrichment stimulated growth and yield in the field substantially exceeded the typical stimulation seen in controlled environments (Kimball and Mauney, 1993). Interpretation was difficult, however, because in these experiments there was a significant effect of the open-top chambers themselves that might have altered the results.

One of the greatest world-wide limitations to crop yield is the occurrence of water stress (Boyer, 1982). Thus an additional question of great interest is the influence of water stress on crop responses to CO_2. Most research on this topic has also been carried out in controlled environments (Sionit et al., 1980; Wulff and Strain, 1982; Morison and Gifford, 1984; Tolley and Strain, 1984). In general, high CO_2 slowed transpiration and reduced the severity of the water stress; as a result, CO_2 enrichment exerted a larger stimulatory effect on water-stressed plants than on unstressed plants (Dahlman et al., 1984; Dahlman, 1992). This subject is especially complex because of the dual effect of CO_2 enrichment on photosynthetic assimilation and on transpiration; again, applicability of these findings to the field needs to be demonstrated. Kimball and Mauney (1993) studied water stress–CO_2 interactions in open-top field chambers. As with the main effects of CO_2 enrichment, the results again differed from those in controlled environments, i.e. water stress did not increase the relative stimulation by CO_2.

The free-air CO_2 enrichment (FACE) system offers a means of studying direct CO_2 effects, and CO_2–environment interactions, on crop growth under natural conditions in an open field. Here we report studies of the water relations of CO_2-enriched cotton at two levels of water supply.

2. Materials and methods

All experiments were carried out at the University of Arizona Maricopa Agricultural Center (33.07°N, 111.98°W, elevation 358 m). Seeds of cotton (*Gossypium hirsutum* L., cv. 'Deltapine 77') were planted on 16 April 1991 (day of year (DOY) 106) in rows 1.02 m apart in a 4 ha field with a drip irrigation system 0.18–0.24 m below the surface. The soil was a reclaimed Trix clay loam (fine-loamy, mixed (calcareous), hyperthermic Typic Torrifluvents). The field was divided into four blocks, each of which was split into two sub-blocks. One of the two sub-blocks was supplied with ample irrigation water throughout the cropping period ('wet' treatment; 1048 mm of water). The amount of water to be supplied was estimated as potential evapotranspiration from a grass reference crop (ET_0) multiplied by LAI (leaf area index)/3 for LAI < 3; otherwise ET_0. Deficit irrigations were initiated in the other sub-block on DOY 140, with water applied thereafter at 0.67 of the amounts for the wet treatment ('dry' treatment; 792 mm of water). Total precipitation from planting to harvest was 41 mm. Details of crop growth have been given by Mauney et al. (1994).

Within each block, two rings of 25 m diameter each spanned the border between sub-blocks. One ring was a FACE array of vent pipes to maintain a CO_2-enriched atmosphere. The other was an unenriched control ring. The distance between rings in each direction was 100–150 m. CO_2 was injected into the FACE plots from 26 April (DOY 116) to 16 September (DOY 259) between 05:00 and 19:00 h at a set point of 550 μmol mol^{-1}. The system for maintaining CO_2 at the set point has been described elsewhere (Lewin et al., 1994). The ambient concentration of CO_2 in the control rings was also monitored, and averaged 370 μmol mol^{-1} (Nagy et al., 1994).

Leaf water potential was estimated as the xylem pressure potential with a Scholander pressure chamber (Soil Moisture Equipment Corporation, Santa Barbara, CA), following procedures of Bhattacharya et al. (1991). Briefly, the most recently expanded mainstem leaf (fourth or fifth leaf) of a plant was shaded, enclosed in a plastic bag, and then excised with a sharp razor blade. The excised leaves in closed bags were placed in a humidified cooler chest and transported to a nearby laboratory for immediate measurement (Bhattacharya et al., 1990). For each sub-block, measurements were replicated on leaves excised from eight plants selected randomly.

Stomatal conductance and leaf transpiration rate were determined with a Li-Cor LI-1600 steady-state porometer (Li-Cor Instruments, Lincoln, NE). For each leaf, abaxial and adaxial measurements were made sequentially and added. For each sub-block, measurements were replicated with 8–10 leaves.

Apparent hydraulic conductance of the plants was estimated by a procedure dependent upon leaf water potential and transpiration rate. At steady state, the relationship between leaf water potential and transpirational flux can be expressed as

$$J = L\Delta\Psi \tag{1}$$

in which J is water flux, L is the hydraulic conductance between soil and leaf, and $\Delta\Psi$ is the water potential difference between the two sites (Radin et al., 1991). L was

estimated as the slope of a plot of J on $\Delta\Psi$, assuming that $\Psi_{soil} = 0$. Variation in J and $\Delta\Psi$ was generated by time of day, with measurements taken from dawn to midday. Single-leaf transpiration rate was assumed to represent whole-plant flux (Radin et al., 1991).

Plants were harvested for estimation of crop dry weight from a specially designated 'destructive harvest' area of the plots (Mauney et al., 1994). They made up one-third of the plants from 3 m of row on each harvest date. To avoid sampling bias, sections of row and individual plants were selected for harvest on DOY 130, while the plants were still seedlings. Tagged individual plants were harvested, separated into components, and dried for 10 days at 60°C to obtain dry weights of roots, stems, and bolls. All data reported are averages of the four blocks (replications), together with their corresponding standard errors. We also estimated the probabilities of differences between treatments (t-test).

3. Results and discussion

3.1. Leaf water relations

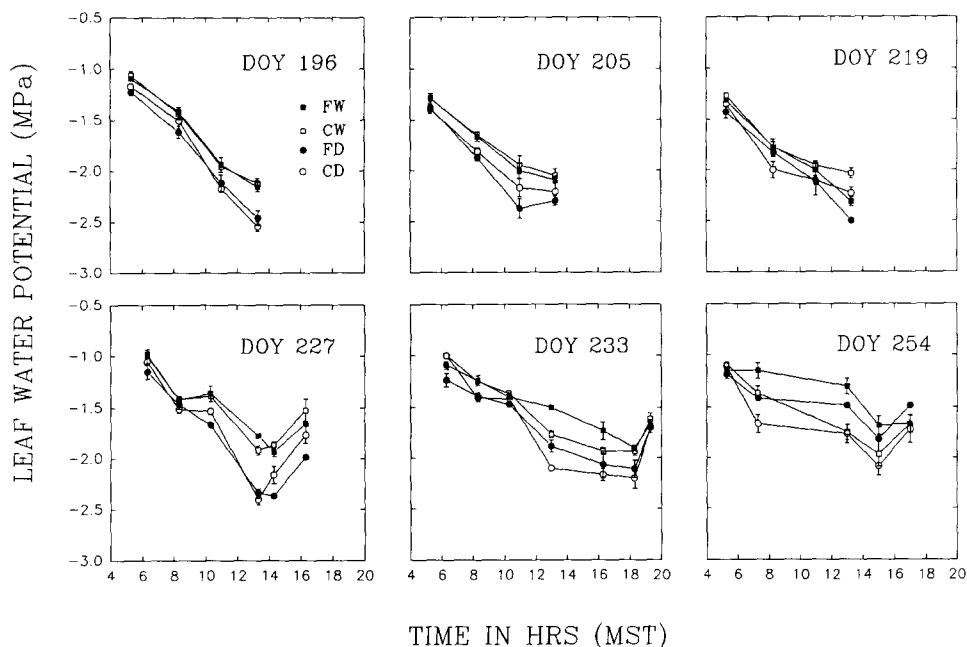Leaf water potentials at 06:00 h Mountain Standard Time (MST) (predawn)

Fig. 1. Diurnal leaf water potentials of cotton plants on six selected days in 1991 from day of year (DOY) 196 to 254. Values are shown ±SE ($n = 8$); for points shown without error bars, the SE was less than the width of the symbol. FW: FACE (enriched CO_2) wet; CW: control (ambient CO_2) wet; FD: FACE dry; CD: control dry.

ranged from −1.0 to −1.2 MPa on 15 July (DOY 196), then decreased by about 0.2 MPa to a seasonal minimum in August before increasing again in September (DOY 254) (Fig. 1). Effects of watering regime and CO_2 elevation on predawn water potentials were minimal. Although watering regimes did not affect predawn water status, they did affect growth rates, as plants in the dry treatments were smaller than those in the wet treatments (Mauney et al., 1994). Presumably growth was responding to subtle differences in plant water status that were not reflected in the predawn water potentials, but which caused the plants to adjust their size to accommodate the available water supply.

Although CO_2 and water treatments had little effect on predawn water potential, both watering regime and CO_2 supply affected daytime water potentials (Fig. 1). In dry treatments before DOY 254, midafternoon potentials were consistently 0.2–0.5 MPa lower than those from wet treatments. By DOY 254, however, differences were much smaller. This change in the magnitude of treatment differences coincided with the onset of higher overall water potentials throughout the day: on DOY 254, the minimum water potentials of plants in the various treatments were 0.3–0.5 MPa higher than on DOY 233 (Fig. 1).

Effects of elevated CO_2 on water potentials differed from the effects of watering regime. Differences between CO_2 levels were small and inconsistent until DOY 227, when water potentials began to be maintained higher in the FACE treatments than
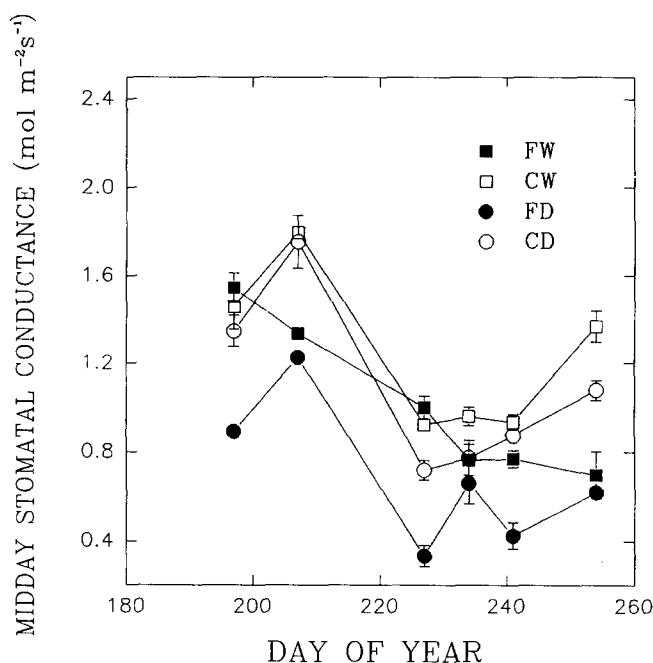

Fig. 2. Stomatal conductances of young expanded leaves of cotton plants at midday. Values are shown ±SE (n = 8); for points shown without error bars, the SE was less than the width of the symbol. Treatment designations as in Fig. 1.

in the control treatments (Fig. 1). By DOY 254 the difference was large (around 0.3 MPa) and occurred throughout the daylight hours (Fig. 1).

In the wet treatments, these effects of CO_2 on water potentials corresponded to effects on stomatal conductance and transpiration rate. Elevated CO_2 suppressed midday stomatal conductance (Fig. 2) and single-leaf transpiration (Fig. 3) by DOY 233, with differences increasing after that time. These data imply that in the wet treatments late in the year, CO_2 effects on leaf water potentials were inversely related in straightforward fashion to the rate of water loss from leaves by transpiration.

In contrast to the wet treatments, in the dry treatments elevated CO_2 consistently and strongly suppressed stomatal conductance throughout the period monitored, with a large effect already evident by DOY 196, the first day of measurements (Fig. 2). Diurnal single-leaf transpiration rates on 3 days (DOY 227, 233, and 254) tended to follow these changes in stomatal conductance (Fig. 3). Elevated CO_2 in the dry treatment raised the leaf temperature by 1–1.5°C (P.J. Pinter, Jr, personal communication, 1993), also indicating decreased transpiration. However, in the dry treatments, the greater stomatal response to elevated CO_2 did not result in higher water potentials until late in the season. Thus in the dry treatments for most of the season, CO_2 effects on leaf water potentials were unrelated to its effects on stomatal conductance and single-leaf transpiration, possibly because another CO_2-dependent factor may have compensated for the stomatal closure. We speculate that in the dry treatments, elevated CO_2 decreased the plant's ability to take up water from the soil, as it partially closed the stomata, leaving leaf water potential unchanged for most of the season.

The trends in water potentials reported here are similar to those found in the 1990 field season (Bhattacharya et al., 1991). In general, previous work also indicated no large or sustained effects of elevated CO_2 on water potentials. As in this study, effects of watering regime were also relatively small for most of the season, compared with effects on plants grown in greenhouses, open-top chambers (Bhattacharya et al., 1990), and a phytotron (see Bhattacharya (1993) for references).

The treatment effects on stomatal conductances also resembled those found during the 1990 field season (Hileman et al., 1994). In 1990, the effect of CO_2 enrichment on conductance was much larger in August (mean decrease of 31%) than in July (mean decrease of 12%). In both months, Hileman et al. noted a non-significant trend for the dry plots to respond more to CO_2 enrichment than the wet plots; they also saw an effect of CO_2 on stomata in June, but the conductances were much lower than later in the season.

Both predawn and midafternoon leaf water potentials reached their seasonal minima in August, as much as 0.4 MPa lower than in late September (Fig. 1). The most likely explanation for this late-season change involves changes in atmospheric evaporative demand. From DOY 227 to DOY 254 the maximum daily temperature decreased from 38–40°C to 30–31°C, and atmospheric vapor pressure deficit decreased from 4.5–6 kPa to 3–4 kPa. The difference between wet and dry treatments in midafternoon water potentials was also greatest on DOY 227 (Fig. 1). Soil water deficit was significantly greater in the dry treatments than the wet treatments
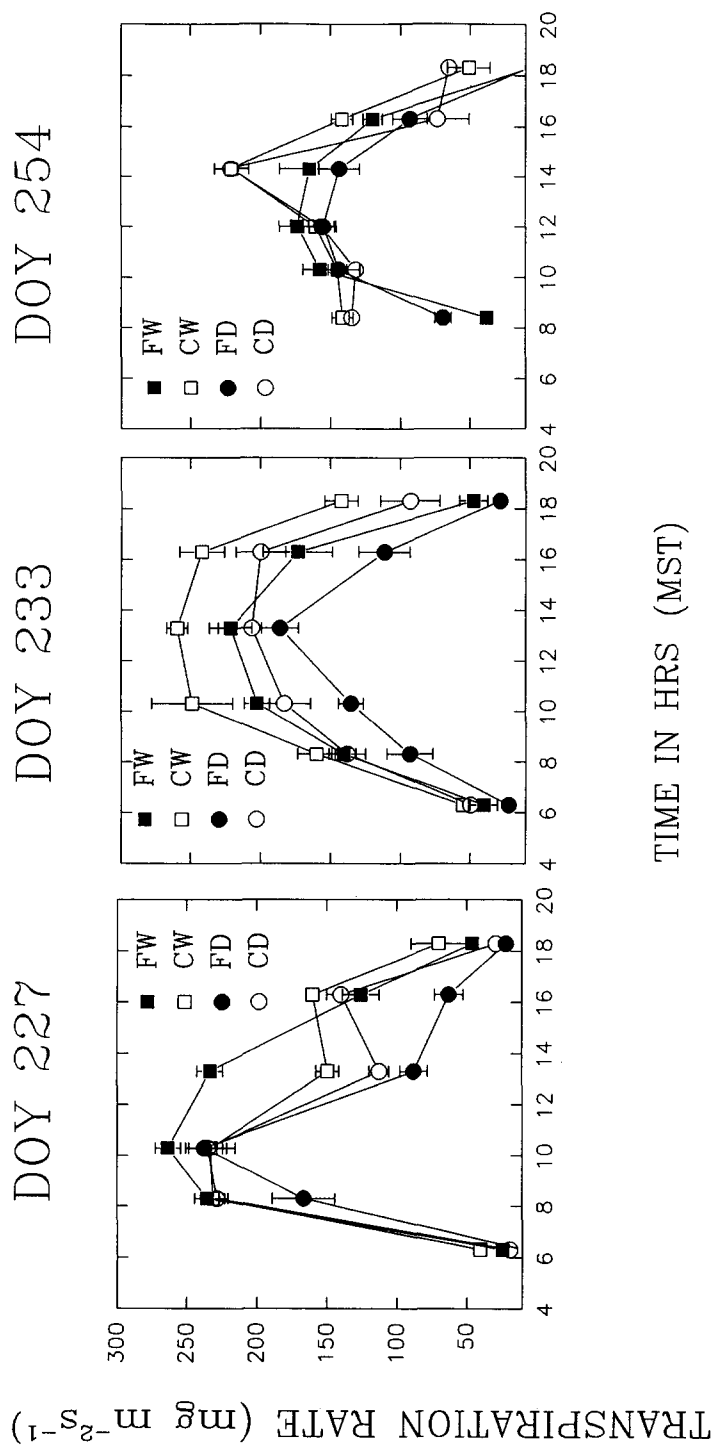
Fig. 3. Diurnal changes in single-leaf transpiration rates of young expanded leaves of cotton plants on three selected days in 1991. Values are shown ±SE ($n = 8$); for points shown without error bars, the SE was less than the width of the symbol. Treatment designations as in Fig. 1.

(Hunsaker et al., 1994). Seasonal changes in the water potential differential between wet and dry treatments are consistent with the combination of restricted water supply and maximum demand in August.

3.2. Biomass accumulation and partitioning

Elevated CO_2 increased biomass accumulation substantially in both the wet and the dry treatments (Fig. 4). The stimulation was important early in the season, leading to increases in biomass by mid-July (DOY 196). In the second half of the season, growth rate of the control plants slowed after DOY 240 in the wet treatment and DOY 220 in the dry treatment (Fig. 4). CO_2 enrichment extended the period of rapid growth, essentially eliminating the late-season slowdown. Overall, CO_2 enrichment increased harvested end-of-season biomass 39% in the wet treatment and 34% in the dry treatment (Fig. 4).

In numerous other experiments, elevated CO_2 stimulated growth of C_3 plants more under water-stressed conditions than under well-watered conditions (Gifford, 1979; Tolley and Strain, 1984; Paez et al., 1984; Conroy et al., 1986, 1988). In many cases, these results were obtained with plants grown in pots in controlled environments, and their applicability to the field was untested. Elevated CO_2 stimulates profuse root growth in the field (Rogers et al., 1992; Prior et al., 1994), a response that might alter plant water relations. In field experiments in open-top chambers, Kimball and Mauney (1993) found no increase in responsiveness to CO_2 as a result of water stress. Our data confirm and extend these latter findings to an open-field FACE array.
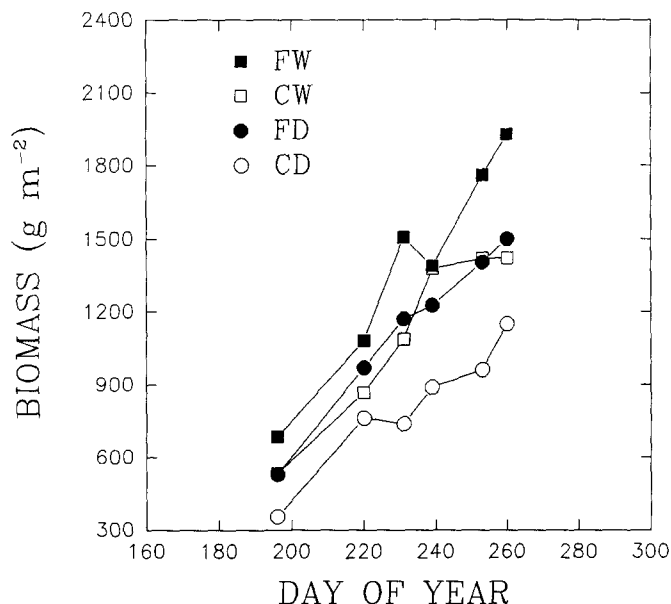

Fig. 4. Seasonal accumulation of biomass of the cotton crop in 1991. Plant population varied from 10 to 12 m^{-2}. Treatment designations as in Fig. 1.

3.3. Apparent hydraulic conductance

Even in the wet treatments which were not subjected to soil moisture stress, leaf water potential and stomatal conductance (transpiration rate) fluctuated during the season (Figs. 1 and 2). Midday water potentials reached a minimum in August, despite conductances at that time as low as half those displayed earlier in the year (Fig. 2) and transpiration rates that were also greatly reduced. These changes imply that the hydraulic conductance of the soil–plant system may have also been at a minimum during August. Radin et al. (1992) associated the seasonal minimum of hydraulic conductance of the soil–plant system (which they assigned to the plant and labelled 'apparent hydraulic conductance') with a high rate of boll filling. They hypothesized that massive partitioning of assimilates to bolls might lead to root degeneration during August. In the present experiments, apparent hydraulic conductance was estimated as the slope of the relationship between transpiration rate and leaf water potential. There was little effect of CO_2 enrichment on this slope (Fig. 5), indicating that almost none of the CO_2 effects on leaf water potential were related to water uptake and transport to the leaf. Instead, the major effects of CO_2 on plant water relations were exerted at the level of water loss from the leaf, i.e. on the stomata.

Elevated CO_2 suppressed stomatal conductance and transpiration rate much more in the dry treatment than in the wet treatment, especially in July (Figs. 2 and 3), but there was no comparable water-stress-dependent effect of CO_2 on the leaf water potentials (Fig. 1). These results imply a possible effect of CO_2 on apparent hydraulic conductance under water stress conditions. No specific conclusions can be drawn from such observations, as the estimation of apparent hydraulic conductance depends upon an assumption that water is freely available in the soil (Radin et al., 1991). The occurrence of water stress in the dry treatments violates this assumption. Nonetheless, the failure of CO_2 enrichment to increase leaf water potential as it decreases stomatal conductance in the dry treatment is a significant observation. This finding may be related to the lack of a CO_2 enrichment–water stress interaction on biomass production in the field (Fig. 4).

4. Conclusions

(1) In a FACE experiment, CO_2 enrichment decreased stomatal conductance of fully irrigated field-grown cotton only toward the end of the season (DOY 233 and later). Before DOY 233, it had little effect. CO_2 enrichment strongly decreased stomatal conductance of deficit-irrigated cotton throughout the season.

(2) Regardless of irrigation level, CO_2 enrichment increased leaf water potentials toward the end of the season, but otherwise had little effect. There were no consistent measurable effects of CO_2 on apparent hydraulic conductance of fully irrigated plants.

(3) CO_2 enrichment increased above-ground biomass production by 39% under full irrigation and 34% under deficit irrigation. The failure of water stress to increase CO_2 responsiveness is similar to previous results from experiments in open-top chambers.
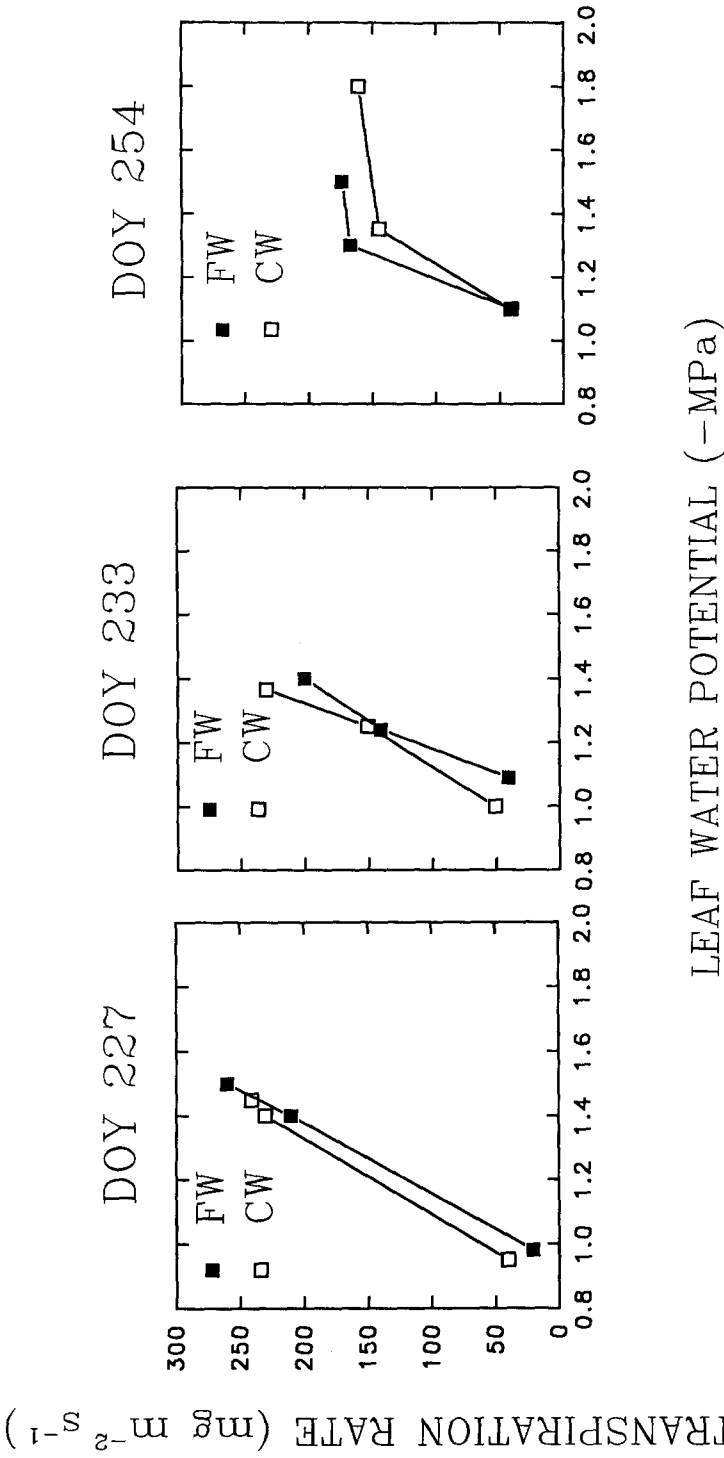
Fig. 5. Relationship of single-leaf transpiration rate to leaf water potential on three selected days in 1991. Variation was generated by time of day, with measurements made from before dawn to midday. The slope of the relationship is an estimate of apparent hydraulic conductance of the plant. Treatment designations as in Fig. 1.

Acknowledgments

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